The impact of ecosystem connectivity on coral reef resilience

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Summary

1. Ontogenetic dispersal of animals has been observed among many ecosystems, but its full ecological significance is poorly understood. By modelling the consequences of ontogenetic reef fish dispersal between Caribbean mangroves and adjacent coral reefs, we quantify the broader implications of ecosystem connectivity for ecosystem function and resilience to climate-driven disturbance.

2. Mangrove-driven enrichment of parrotfish grazing on two coral reef habitats was calculated using empirical data. The consequences of increased grazing were then investigated using a spatial simulation of coral reef dynamics in shallow (depth 3–6 m) and mid-shelf forereefs (depth 7–15 m).

3. The largest increase in grazing occurred in shallow reefs, but was found to have negligible consequences for coral population dynamics.

4. In contrast, relatively weak increases in grazing on deeper reefs had profound consequences: reefs near mangroves were able to experience coral recovery under the most intense hurricane regimes of the Caribbean, whereas those lacking ecosystem connectivity had little capacity for recovery.

5. This surprising result occurs because reefs exhibit multiple stable equilibria and mangrove enrichment of grazing in mid-shelf reefs coincides with a zone of system instability. A small increase in grazing shifted the reef beyond a bifurcation point, thereby enhancing resilience massively. A relatively large increase in grazing in shallow reefs had minimal ecosystem consequence because the grazing levels concerned were more than double the levels needed to exceed the corresponding bifurcation point for this habitat.

6. *Synthesis and applications*. Caribbean mangroves are being deforested at a faster rate than rainforests, yet their protective role against hurricane damage extends not only shoreward to coastal environments but also seaward to increasing the resilience of offshore coral reefs. Specifically, ontogenetic mechanisms of ecosystem connectivity involving parrotfish may increase the probability that coral populations will recover from climate-induced changes in hurricane disturbance. Efforts to arrest mangrove deforestation and restore mangrove habitats are likely to increase the likelihood of recovery of corals on mid-depth (7–15 m) reefs after disturbance. In general, the ecosystem-level consequences of ontogenetic migration do not correspond necessarily to the magnitude of locally observed effects (i.e. the pattern of grazer enrichment exhibited the opposite pattern to that of its consequences for system resilience). Therefore, caution must be exercised when interpreting the functional significance of changes in species abundance for ecosystem process (e.g. grazing pressure and its implications for coral growth and survival). Impacts of shifting abundance or process are perhaps best appreciated using mechanistic ecosystem models.

Key-words: fish, grazing, mangroves, model, ontogenetic

Introduction

Organisms move among ecosystems for a variety of reasons and over many spatial and temporal scales. At large scales, many organisms undertake seasonal migrations to breed, avoid unfavourable environmental conditions or seek ephemeral resources (Webster *et al*. 2002; Sugden & Pennisi 2006). Dispersal

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also occurs with ontogeny and some of the most economically important species, such as the Atlantic sturgeon *Acipenser oxyrhynchus* (Niklitschek & Secor 2005), may occupy three or more ecosystems during their life. The reasons for undertaking ontogenetic dispersal among habitats include requirements for different food sources as the organism grows (Werner & Gilliam 1984; de la Moriniere *et al.* 2003), changing risks of predation with size such that sheltered habitats, where predator foraging efficiency is low, are chosen when the organism occupies its smaller, more vulnerable stages (Shulman 1985; Laegdsgaard & Johnson 2001), and a need to reproduce in habitats which offer the greatest dispersal or highest survival of larvae.

Although ontogenetic dispersal occurs in many environments, the net consequences of such ecosystem connectivity are only beginning to be understood. Perhaps the most important implication of such connectivity is that the functioning of an ecosystem, such as its productivity, is not independent from its spatial context in the landscape: connected ecosystems in close proximity may behave differently to more isolated systems. A particularly striking example was reported for Caribbean mangrove forests which are being rapidly deforested (Valiela, Bowen & York 2001), yet are connected to neighbouring coral reefs through the process of ontogenetic dispersal. Many coral reef fish utilize mangroves as nurseries during their juvenile phase and then migrate seaward to their adult reef habitat (Nagelkerken *et al.* 2000). In a recent natural experiment, the net impact of losing rich mangrove resources (defined as having a perimeter of *Rhizophora* prop roots of < 70 km within a region of 200 km^2) was quantified for the biomass of adult fish (Mumby *et al.* 2004). The largest herbivorous fish in the Atlantic, the rainbow parrotfish *Scarus guacamaia*, was found to have a functional dependence on mangroves and its distribution was confined to shallow reefs neighbouring mangroves. Furthermore, the biomass of a small but common grazing species, *Scarus iserti*, was enriched significantly when reefs were connected to mangroves (42% increase over non-mangrove systems). Therefore, empirical data show that mangrove connectivity enhances the biomass of two grazing reef fish on neighbouring coral reefs. Because grazing influences the cover of macroalgae on reefs (Williams & Polunin 2000; Kramer 2003; Mumby *et al.* 2006a), and macroalgae compete for space with corals (McCook, Jompa & Diaz-Pulido 2001), these empirical data raise the intriguing possibility that ecosystem connectivity may enhance indirectly the resilience of coral populations to disturbance (i.e. mangrove-driven increases in grazing may increase the likelihood that corals will recover from disturbance and enhance their rate of recovery). Here, we hypothesize that the response of coral populations to increased grazing will be greater in habitats which benefit most strongly from mangrove-reef connectivity. We examine this hypothesis by extending a spatial simulation model of coral reefs to examine whether observed levels of ecosystem connectivity have the potential to enhance the resilience of corals to climate-driven disturbance. We conclude that demographic processes (ontogenetic dispersal) can alter ecosystem function in a profound but non-intuitive manner.

Methods

GENERAL OVERVIEW

A simulation model of coral reef dynamics was used to investigate the ecosystem-level consequences of elevated parrotfish densities in reefs connected to mangrove ecosystems (Fig. 1). The original model was published in 2006 (Mumby 2006; Mumby *et al.* 2006b) and then modified in 2007, and found to reproduce reef dynamics faithfully when tested against an independent 20-year empirical data set from Jamaica (Mumby, Hastings & Edwards 2007). These earlier formulations of the model ignored mangrove connectivity and considered only a single habitat: mid-depth forereefs of depth 7–15 m. Here, the model has been extended to incorporate the impacts of mangrove connectivity and a second, shallow forereef habitat of depth 3–6 m. Detailed modifications to the model are described below, but in summary the modelling of shallow reefs required the incorporation of new empirical data on grazer biomass, coral growth rates and algal population dynamics. Mangrove impacts on grazing differed with depth because the biomass of two parrotfish species (*S. guacamaia* and *S. iserti*) was elevated in shallow water, whereas only *S. iserti* benefited in deeper water.

BASIC MODEL STRUCTURE (MID-DEPTH FOREREEFS WITHOUT MANGROVES)

A simulation model was originally designed to represent mid-depth forereefs which typically harbour the highest biomass and diversity of reef organisms (Mumby *et al.* 2006b). Because white band disease has depleted populations of large, branching corals (Aronson & Precht 2001), stylized massive growth forms of coral were simulated together with rates of recruitment, growth, reproduction and mortality. The model is a square lattice of 2500 cells, each of which approximates 0·25 m^2 of reef, and can be occupied by a mixture of living and dead substrata (Table 1). Although the reef has a continuous (toroidal) lattice of 2500 cells, the lattice structure merely helps to define probabilistic rules of coral recruitment and vegetative algal growth. Individual cells comprise multiple coral colonies and algal patches, so interactions occur at colony scales as they do *in situ*. The reef has continuous boundaries, arranged as a torus. Corals can recruit to individual patches of cropped algae (which in this model harbour little sediment) but not macroalgae. Macroalgae emerge when dead coral is not grazed and also spread vegetatively. While macroalgae can cause limited levels of coral mortality, the primary mode of vegetative growth occurs opportunistically over coral that experienced mortality from some other cause (e.g. scour during hurricanes).

The modelling of grazing is carried out at two scales. First, the simulation model requires an overall grazing impact, which defines the proportion of reef maintained effectively in a cropped algal state during a 6-month iteration of the model. In other words, given the overall balance between algal production and grazing, the grazing impact is the proportion of a reef that is grazed sufficiently intensively that algae are kept in a cropped state rather than developing into a macroalgal canopy within a 6-month period. A '6-monthly' value of grazing impact is needed for model implementation because many of the parameters, such as the vegetative growth of corals and macroalgae, are derived at monthly scales that are many orders of magnitude greater than the instantaneous grazing rate of fishes (seconds). Parameters for the grazing impact of parrotfish were derived from field studies with durations of months to years (see Appendix S1, Supplementary material) and have a maximum value of 30–40% 6 months^{-1}, depending on reef productivity. Given that such field
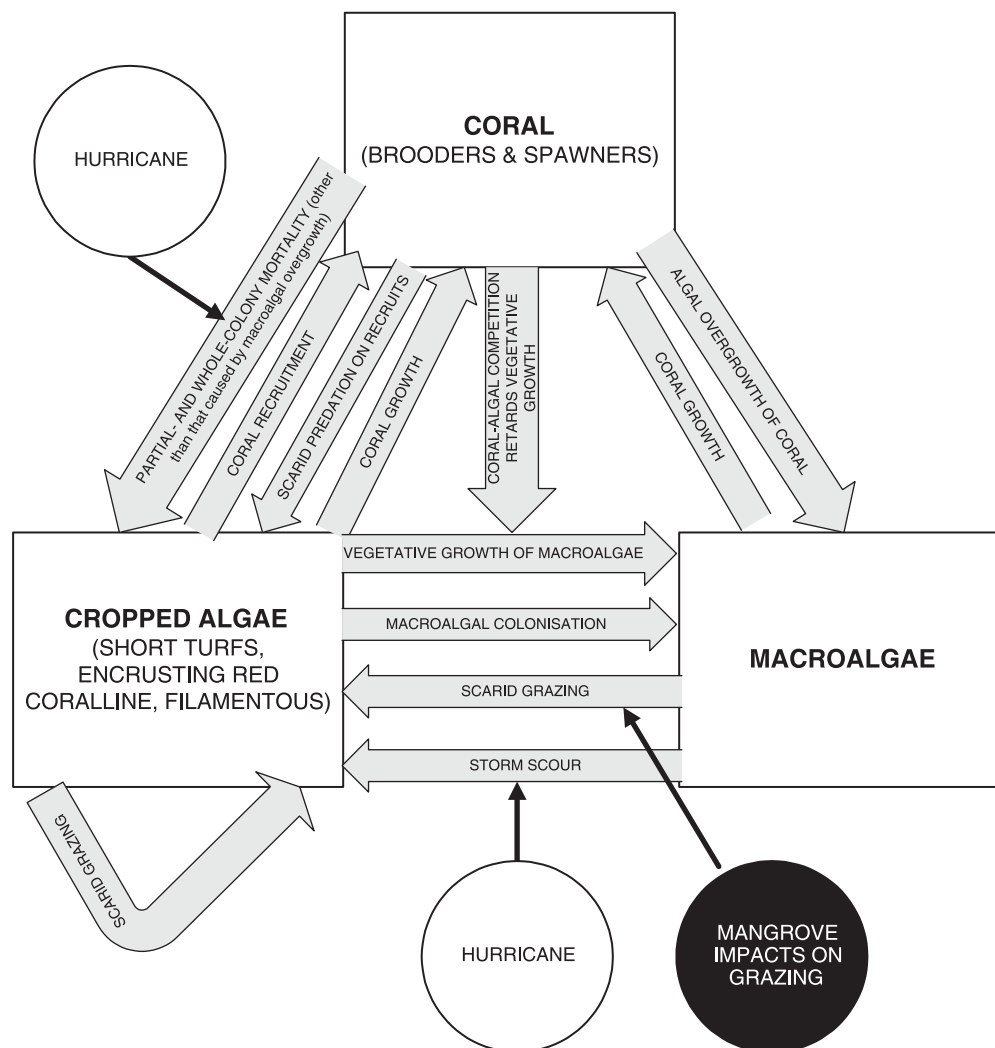
Fig. 1. Schematic of processes included in the simulation model of coral reef dynamics.

Table 1. Contents of individual cells (0·25 m²) within the model. All substrata represented as area (cm²)

Substratum	Constraints	Range (cm²)
Brooding coral (e.g. *Porites astreoides*) (BC)	Up to three individuals per cell	$1 \leq BC \leq 2500$
Spawning coral (e.g. *Siderastrea siderea*) (SC)		$1 \leq SC \leq 2500$
Cropped algae [filamentous, coralline red algae and short turfs (< 5 mm height)], 0–6 months (A6)		$0 \leq A_6 \leq 2500$
Cropped algae, 6–12 months (A12)		$0 \leq A_{12} \leq 2500$
Macroalgae (e.g. *Dictyota pulchella*, *Lobophora variegata*), 0–6 months (M6)		$0 \leq M_6 \leq 2500$
Macroalgae, 6 + months (M12)		$0 \leq M_{12} \leq 2500$
Ungrazeable substratum (e.g. sand), U	Fills entire cell if present	U = 0 or U = 2500

studies have not been stratified by depth or mangrove connectivity, a second instantaneous model of grazing was used to adjust the grazing impact for these scenarios. The second model measures grazing intensity, which is the instantaneous grazing behaviour of a parrotfish species or community measured as a percentage of horizontal reef area grazed per hour. Intensity is calculated using a model of grazing behaviour sensitive to species, length and life phase (Mumby *et al*. 2006a). Grazing affects all algal classes such that macroalgae are converted to the class 'cropped algae', and grazed cropped algae are maintained in the same state. The effects of fishing, which change the density and size-structure of fishes, have been modelled previously (Mumby *et al*. 2006a), and deplete grazing to 5% of the reef. The urchin *Diadema antillarum* is excluded from simulations because it remains scarce in much of the Caribbean (Kramer 2003), although some recent recovery has been reported (Carpenter & Edmunds 2006).

Competitive interactions between corals and macroalgae reduce the growth rate of each taxon. Corals are subjected to size-dependent fecundity and mortality (see Supplementary material, Appendix S1). All simulations assume no stock-recruitment relationship and corals recruit at maximum levels irrespective of stock size (i.e. up to

four per 0·25 m²). Previous studies with the model have found it to be insensitive to the type of stock-recruitment relationship used, largely because of such high post-settlement mortality (Mumby 2006). Individual cells in the lattice are updated in random sequence. Acute disturbance occurs from hurricanes. Sensitivity analyses reveal that model predictions are robust to stochastic variation in parameter values (Mumby, Hastings & Edwards 2007).

NEW PARAMETERIZATION FOR SHALLOW CORAL REEFS (WITHOUT MANGROVES)

Three processes were adapted to represent shallow reefs. Higher light levels in shallow water affect the growth rates of corals and macroalgae. Huston (1985) examined the growth rates of spawning and brooding coral species with depth. Based on these data, the growth rate of spawners was left at 9 mm year⁻¹, but that of brooders was increased from 8 mm year⁻¹ to 15 mm year⁻¹. New data were collected to adjust the vegetative growth rate of macroalgae (principally *Lobophora variegata*) to shallow reefs which have higher productivity. The dynamics of 24 newly established patches of *Lobophora* were monitored at depths of 5 m and 9 m for a period of 8 months in 2005. All data were collected from caged experiments on the seaward forereef of Glovers Atoll, Belize (Mumby, Foster & Glynn Fahy 2005). The maximum observed growth rates were found to be 1·5 times greater in shallow water (0·35 cm² day⁻¹ vs. 0·23 cm² day⁻¹) and this growth enhancement was included in the model (i.e. probability of macroalgae colonizing a cell, P_m, increased by 50% where the parameterization for mid-shelf reefs sets P_m as a linear function of the proportion of macroalgae in a surrounding four-cell neighbourhood). While algal growth rates were found to increase in shallow water, algal colonization rates showed no significant difference with depth (H. Renken, personal communication) and were therefore left unchanged in the shallow water model.

Grazing impact was adjusted using new field data on parrotfish community structure from both mid-shelf and shallow reef habitats in Belize, Bonaire and the Bahamas. The mean total grazing intensity, including all parrotfish species, in shallow reefs was substantially greater than that of mid-shelf reefs in the Bahamas (0·30% of reef h⁻¹ vs. 0·22% h⁻¹). Scaling the net 6-month impact of such grazing from that of mid-shelf reefs, where 30% of the reef can be grazed 6 months⁻¹, to shallow reefs gives a net grazing impact of 41% 6 months⁻¹. However, shallow *Montastraea*-dominated reefs have a lower structural complexity than mid-shelf reefs, which means that the surface area of substratum per unit horizontal area of reef is lower (*n* = 45 sites). With less reef to graze, the effective grazing intensity of parrotfish is increased. Assuming that the change in complexity, measured as the mean of maximum vertical relief within 401 m² quadrats per site (74 cm vs. 62 cm in mid-shelf and shallow reefs, respectively), is related linearly to the efficacy of scarid grazing, the net impact of grazing in shallow reefs rises to a final value of 49% of the reef per 6 months. That the impacts of grazing are greater in shallow reef habitats, even in the absence of mangroves, is borne out by field data (Fig. 2, r^2 = 0·59, P < 0·01, percentage macroalgal cover = 4·8 × depth –15).

The parameterization for severe hurricanes was assumed to hold between habitats. While this could underestimate the mortality experienced by branching corals in shallow reefs (which fragment easily), disease has reduced severely the abundance of branching *Acropora* spp. in many Caribbean reefs. At the depths implied by the model, much of the hurricane-induced mortality on corals is caused by sand scour, which is putatively less depth-dependent than direct mechanical breakage (Mumby 1999).
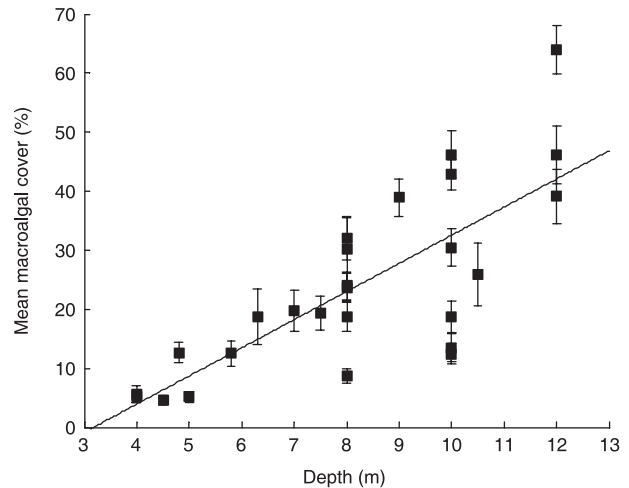

Fig. 2. Relationship between depth and mean macroalgal cover at 26 forereef sites on Glovers Reef (Belize) acquired 7 years after Hurricane Mitch. Bars denote standard errors.

IMPACT OF MANGROVE CONNECTIVITY ON GRAZING IN MID-SHELF REEFS

Mangrove connectivity increased the biomass of *Scarus iserti* in Mesoamerica by 42%, but did not influence the density of any other parrotfish species in this habitat (Mumby *et al.* 2004). The resulting shift in biomass is responsible for a 50% increase in the grazing intensity of *S. iserti* in rich mangrove systems (0·14% h⁻¹ to 0·21% h⁻¹ in depauperate and rich systems, respectively, averaged across three atoll-sized systems in each treatment). Although *S. iserti* is one of the smallest species of parrotfish, typically reaching a total length of around 20 cm, it is also the most abundant. On average, *S. iserti* comprises 20% of the total parrotfish grazing intensity on reefs without mangrove connectivity (averaged from 30 reef sites in the Bahamas and Belize). If the contribution of *S. iserti* to the total grazing impact in mangrove-depauperate systems (i.e. 30% of the reef 6 months⁻¹) is isolated (i.e. 20% of 30, giving six) and enriched by 50% (i.e. three units of grazing impact), the total effective grazing impact in mangrove-enriched mid-shelf reefs rises to 33% 6 months⁻¹. In other words, mangrove connectivity increases the total grazing impact of parrotfish communities on mid-shelf reefs by ~10% (from 30% to 33% of the reef).

IMPACT OF MANGROVE CONNECTIVITY ON GRAZING IN SHALLOW REEFS

The study of mangrove impacts in Mesoamerica did not quantify specifically the biomass of *S. iserti* in shallow reefs (Mumby *et al.* 2004). However, *S. iserti* is found commonly in this habitat even if it comprises only approximately 4% of total parrotfish grazing (based on data from the Bahamas). Therefore, the most parsimonious assumption is that the extent of mangrove influence in shallow reefs matches that of mid-shelf reefs (i.e. causing a 50% increase in the grazing impact of this species). The grazing impact of *S. iserti* before mangrove enrichment is two based on a 4% contribution to a total grazing impact of 49% 6 months⁻¹ (i.e. 4% of 49 ~ 2). Therefore, enrichment to *S. iserti* results in a total increase in grazing impact of 1% units (50% enrichment of 2). Note that this may be a conservative estimate of enrichment because other (non-grazing) species observed to experience mangrove enrichment, such as members of

Haemulidae, typically experience greater enrichment in shallow reefs than on mid-shelf reefs (Mumby *et al*. 2004).

The main impact of mangroves on shallow reefs is the support of adult *S. guacamaia* (Mumby *et al*. 2004; Dorenbosch *et al*. 2006). This massive scarid can often attain 80 cm in length and, as grazing impact is a power function of body length (Bruggemann *et al*. 1996), its grazing is considerable. As individual fish could not be harvested, the grazing impact of *S. guacamaia* was modelled by assuming that allometric scaling of bite size with body size held within genera. Bite rates and home ranges were determined by following eight individuals in Bonaire and Belize for a 2-min period. Observations of bite rate had a reasonably high precision [standard error (SE)/mean] of less than 20% (Andrew & Mapstone 1987). A home range of 1600 m[2] (estimated conservatively) is larger than that of many other scarids (Mumby & Wabnitz 2002), and grazing by this species represents ~14% of the total grazing intensity measured for mangrove depauperate systems (0·041% h[-1] of 0·302% h[-1]). Increasing the total grazing impact for shallow reefs (49% 6 months[-1]) by this proportion yields a new impact of 56% 6 months[-1]. Combining the contributions of both *S. guacamaia* and *S. iserti* to grazing in mangrove-rich shallow reefs gives a total grazing impact of 57% 6 months[-1], which is an overall enrichment of 16% (eight/49).

MODELLED SCENARIOS

The effects of mangrove-enriched grazing were studied using two approaches. The first removed acute disturbance and determined equilibrial levels of coral cover after a 50-year simulation. Chronic levels of whole-colony mortality were applied equally to juvenile and adult corals and increased to 0·4 per annum. Partial-colony mortality was left at constant background levels (see Supplementary material, Appendix S1). The second scenario simulated major hurricane events with a long-term incidence of once per decade and once every 20 years, roughly corresponding to environmental conditions in the Bahamas and Belize, respectively (Gardner *et al*. 2005). Note that while the long-term incidence of hurricanes was fixed their implementation was stochastic, such that higher and lower frequencies occurred over shorter time-scales as they do in nature (Webster *et al*. 2005). The net outcome of hurricane-induced disturbance and recovery on total coral cover was evaluated after a 50-year simulation. Note that while two types of coral were simulated, results are reported only for total coral cover, because the observed recruitment rate of spawners does not allow for persistence and the results are dominated by those of brooding species (the enigmatic population dynamics for spawners will be explored elsewhere). Each 50-year simulation was repeated 10 times for each scenario and mean results reported. Standard errors are reported simply to convey the variation in model simulations for hurricane scenarios, and no statistical importance is implied.

Results

RESPONSE OF REEFS TO MANGROVE-DRIVEN INCREASES IN GRAZING

In a first simulation, juvenile (diameter 61–250 cm[2]) and adult corals (diameter > 250 cm[2]) were subjected to various levels of chronic mortality (0·01–0·40 per year) and the equilibrial level of coral cover determined after 50 years. The response of reefs to elevated grazing differed dramatically between habitats. Corals on shallow reefs responded linearly and negatively to the rise in coral mortality rate (Fig. 3). The survival of coral recruits remained high irrespective of mortality rate,
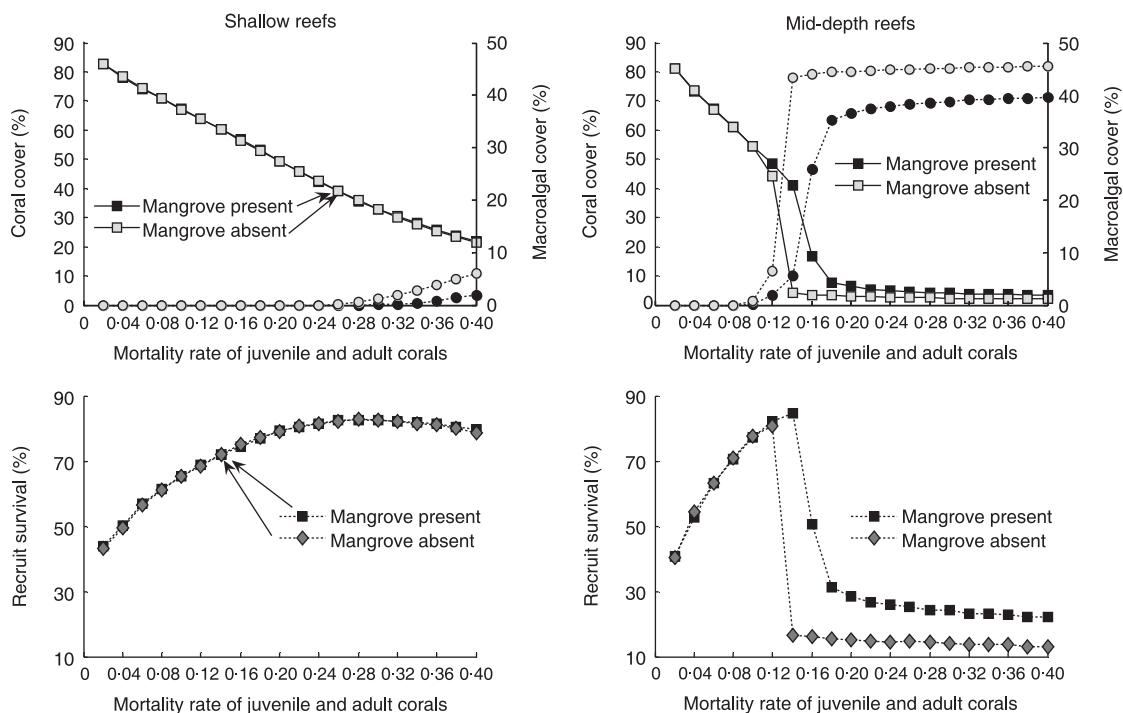

Fig. 3. Response of shallow (left panel) and mid-depth reefs (right panel) to changes in coral mortality rate both with and without mangrove connectivity. Initial coral cover was 30%, divided equally between brooding and spawning taxa. Data presented are equilibrial levels after 50 years and include total coral cover (squares), macroalgal cover (circles) (upper panels) and the survival of a cohort of coral recruits to juvenile size (lower panels).

although the relationship was dome-shaped, increasing initially as rising juvenile and adult mortality liberated space for colonization (Hughes 1985), then reaching an asymptote when space was no longer limiting survival, and finally decreasing as the reduction in coral cover allowed macroalgae to become established and overgrow recruits (Fig. 3). Macroalgal cover remained virtually non-existent until mortality rates exceeded 0·32, at which point it rose gradually. Surprisingly, mangroves had barely any impact on either coral cover or recruit mortality despite causing a 16% increase in grazing in shallow reefs. Mangroves had no discernible effect on the net equilibrial level of coral cover after 50 years of either decadal or 20-year hurricane disturbance (Fig. 4a).

Unlike shallow reefs, the mid-shelf reef did not respond linearly to disturbance and exhibited a sudden shift in community structure, as evidenced clearly by the abrupt phase shift in coral and macroalgal cover once mortality rates exceeded ~ 0·12 (Fig. 3). At lower levels of mortality, coral cover decreased linearly with increasing mortality and macroalgal cover was confined to minimal levels. On reaching a threshold, the coral population crashed and macroalgal cover increased dramatically, reaching asymptotic levels (Fig. 3). The survival of a cohort of coral recruits to adolescence mirrored the step change (Fig. 3). Below the threshold adult mortality rate, recruit survival increased as rising adult mortality led to lower equilibrial levels of coral cover and less coral competition. The survival of recruits then crashed once the mortality threshold was exceeded. Connectivity to mangroves shifted the threshold level of mortality upwards by 2–4%. While this mangrove-driven impact seems modest, it exerted a profound influence on the dynamics of corals subjected to realistic hurricane scenarios.

Under intense decadal hurricane disturbance, reefs with mangrove connectivity managed to achieve high levels of coral cover (> 50%), irrespective of the initial state of the reef (Fig. 4b). Moreover, this mangrove-based impact on resilience was greater than halving the frequency of hurricanes on a mangrove-depauperate reef. In contrast, reefs without mangrove connectivity had little potential for recovery and achieved much lower coral cover. For example, reefs starting at a relatively unhealthy cover of 10% showed little ability to improve after 50 years (Fig. 4b). Even when reefs started at a healthy 30% coral (by today's standards), there was no net increase in cover.

Discussion

Coral reefs with connectivity to mangrove nurseries exhibit increased parrotfish grazing, but the relative magnitude of the enhancement differs among habitats; shallow reefs receive a greater boost to grazing than those at mid-depth. Model simulations found that the consequences of increased grazing on coral population dynamics exhibited a surprising, non-intuitive pattern such that coral populations in shallow reefs were unaffected, whereas those at greater depth responded dramatically to a relatively weak rise in grazing. Therefore, the observed effects of ontogenetic dispersal can diverge dramatically from their ecosystem-level consequences, which implies that caution must be exercised when inferring the consequences of observed patterns of species abundance for ecosystem processes and stability.

The sudden phase shift exhibited by mid-shelf reefs in response to a slight increase in coral mortality implies strongly that the system can exhibit multiple stable states and unstable equilibria (May 1977; Scheffer & Carpenter 2003). Indeed, an analysis of equilibrial coral cover for various levels of grazing revealed two stable community states (one coral-dominated, one macroalgal-dominated) and a region of unstable equilibria defined by an upper and lower bifurcation point (Fig. 2 in Mumby, Hastings & Edwards 2007). At an unstable equilibrium, corals and macroalgae can coexist only under very restricted circumstances. Slight shifts in favour of either competitor result in successful exclusion of the competitor. These mechanisms occur because of feedbacks reinforcing the direction of community shift. For example, a reduction in coral cover permits an increase in macroalgae because grazing becomes dispersed more widely over the benthos and individual patches of algae are regrazed less often. An increase in macroalgal cover not only reduces settlement space for corals, but it increases the mortality rate
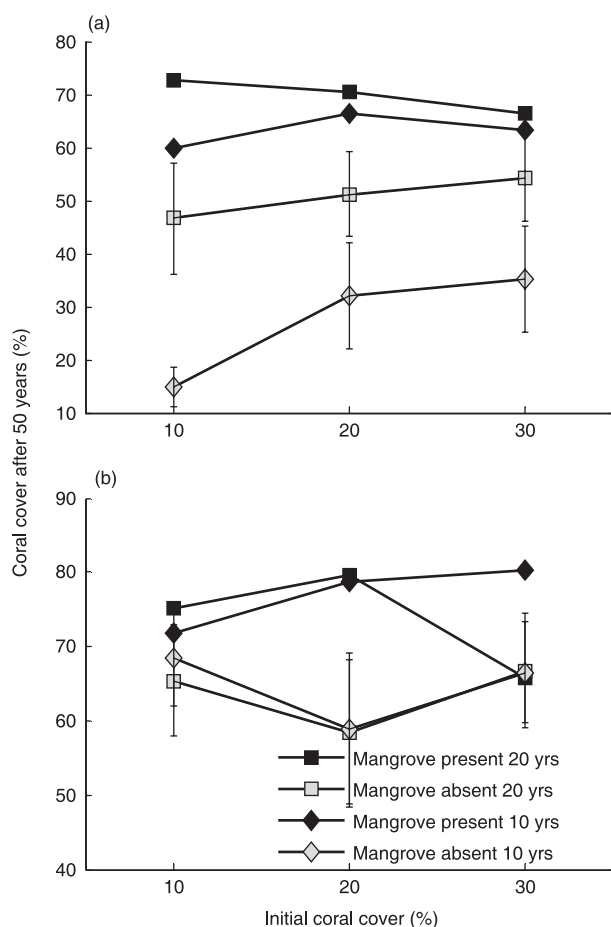

Fig. 4. Response of shallow reefs (a) and mid-shelf reefs (b) to two levels of hurricane disturbance; decadal (denoted 10 years) and every 20 years (denoted 20 years). Standard errors provide a guide to intersimulation variability in cover after 50 years (*n* = 10).

of coral recruits (Bak & Engel 1979; Box & Mumby 2007). A reduction in recruitment may reduce the replenishment of juvenile and adult corals, therefore causing a further decrease in coral cover. This process is reinforced as further reductions in coral cover allow macroalgae to increase, thereby reducing the survival of coral recruits still further and generating a bottleneck in the coral population. This is an emergent property of the model because the mortality rates simulated did not affect coral recruits. Importantly, the kind of phenomena we observe are generic, and do not depend critically upon the specific details of the model (Mumby, Hastings & Edwards 2007). The bifurcation structure, and the dependence on the control parameters, are well-known mathematical phenomena in ecological models with similar overall structure (Angeli, Ferrell & Sontag 2004). In ecological systems, the kind of behaviour we model is similar to that used to explain outbreaks of insects in a generic model (Ludwig, Jones & Holling 1978). The key ingredients are a separation of time-scales combined with density dependence to create the non-linearity.

Grazing determined the vulnerability of the reef ecosystem to sudden phase changes. Mangrove impacts on grazing were significant in mid-shelf reefs because their magnitude coincided with the zone of system instability (Fig. 5). A modest change in grazing was able to shift the reef state beyond its upper bifurcation point, resulting in radical differences in system dynamics. System instability was absent from shallow reefs because grazing impacts of 49% 6 months^{-1} (to 57% with mangroves) exceeded the upper bifurcation point for unstable equilibria, which occurred at a grazing impact of around 24% 6 months^{-1} (Fig. 5). Once grazing levels are high enough to surpass the upper bifurcation point reefs move towards a coral state, although acute disturbances deplete coral cover in the short term. Interestingly, the model predicted that shallow reefs have greater overall resilience than mid-shelf reefs (i.e. the threshold bifurcation of grazing for coral-dominance was

lower in shallow reefs). This result could not have been predicted without the model because the parameterization for shallow reefs included both positive and negative implications for resilience; the increase in coral growth rate would tend to enhance resilience, whereas the increase in macroalgal growth rate would tend to decrease resilience. Clearly, the consequences of increasing coral growth rate outweighed those of allowing faster algal growth.

IMPLICATIONS FOR ECOLOGY AND CONSERVATION

This study provides an important new insight into ecosystem connectivity. By translating demographic consequences of connectivity (increases in fish density) explicitly into an ecosystem process (grazing) and investigating the impact of that process on ecosystem dynamics (resilience), we can contrast the magnitude of demographic effects and ecosystem consequences. Clearly, the observed effects of ontogenetic migration can diverge dramatically from their ecosystem-level consequences (i.e. demographic effects were weakest in mid-shelf reefs but had the greatest impacts on resilience). Therefore, caution must be exercised when inferring the ecosystem-level consequences of observed patterns of species abundance.

The emergence of bistability in mid-shelf reefs strongly reinforces speculation about the permanency of coral degradation (Done 1992; McManus & Polsenberg 2004; Hughes *et al.* 2005) and poses a challenge to coral reef managers. In order to prevent reefs shifting to a macroalgal state, managers must strive to keep grazing levels high and coral mortality rates low. Of course, this is no easy task, given widespread exploitation of grazing fishes (Bellwood *et al.* 2004), continued paucity of the urchin *D. antillarum* in much of the Caribbean (despite recovery in some areas: Carpenter & Edmunds 2006), rising levels of coral disease (Harvell *et al.* 1999) and accelerating climate-driven disturbance (Hoegh-Guldberg 2004). Indeed,
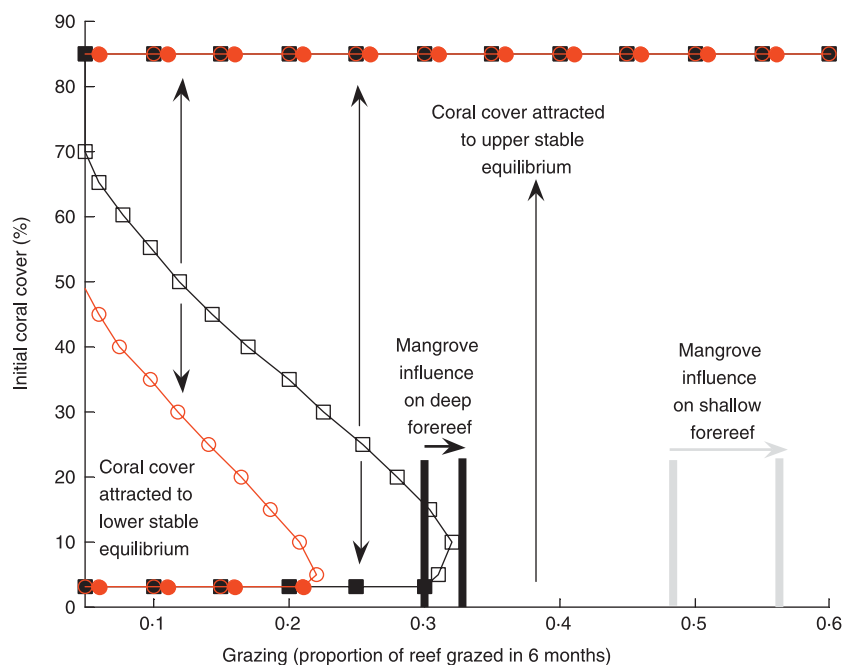

Fig. 5. Hysteresis plot showing stable and unstable equilibria for mid-shelf reefs (black squares) and shallow reefs (red circles). Stable equilibria denoted with solid symbols and unstable equilibria with open symbols. Black arrows show underlying trajectories of coral cover towards stable equilibria. Impacts of mangroves to grazing on mid-shelf and shallow reefs are marked using heavy black and grey lines, respectively.

rates of coral recovery after disturbance are already low in many parts of the Caribbean (Connell 1997; Cote *et al*. 2005; Gardner *et al*. 2005). Although several of these disturbances, such as coral bleaching, were not included in the simulations, this will not influence our conclusions qualitatively because we contrasted whether the mangrove influence on grazing occurred within a zone of system instability (as was the case for mid-depth reefs) or beyond the zone of instability (as was the case in shallow reefs), such that the trajectory of coral cover between successive impacts will always be one of recovery. Increasing disturbance does not affect the relationship between mangrove impact on grazing and the grazing levels at which bifurcation occurs. Of course, a propensity for recovery between disturbances does not imply that the reef will always appear to be 'healthy' with high coral cover, because levels of disturbance could become sufficiently intense to maintain the reef in a state of low cover.

Our conclusions are drawn from a model ecosystem and this naturally raises the question of field testing. Some of the model predictions, such as threshold effects on equilibrial dynamics (Fig. 3), are impossible to test because they simulate reefs for long periods in the absence of acute disturbance phenomena. Even the overall conclusion that mangroves will confer a disproportionately large increase on the resilience of mid-shelf reefs will be difficult to test empirically. This is because individual reef trajectories are subject to the vagaries of many local processes and patchy disturbance. It would be challenging to isolate mangrove-based impacts on reef dynamics without the study being confounded by one of many other factors such as fishing pressure, nutrient supply, bleaching impacts or hurricane impacts. While this does not discount the importance of field testing, our present alternative is to consider the efficacy of the model. All parameters were fitted from empirical studies and while no model can represent the full complexity of the ecosystem, model predictions were found to emulate an independent 20-year record of coral dynamics even when key parameters, such as the ability of algae to overgrow coral tissue, were varied to extreme, albeit published, values (Mumby, Hastings & Edwards 2007). Moreover, recent studies of mid-shelf reefs in the Bahamas found that high levels of parrotfish grazing led to a twofold increase in coral recruitment (Mumby *et al*. 2007), which fits previous model predictions (Mumby 2006).

Although general limitations and sensitivities of the model have been discussed in previous papers, several considerations should be raised. First, the impacts of mangroves on adjacent reefs were confined to the elevation of fish grazing. In some environments, efflux of decomposed organic matter from mangroves may elevate levels of organic nutrients which potentially favours macroalgal growth on reefs. However, most studies have found weak evidence for such nutrient enrichment (Lapointe, Littler & Littler 1987; Ogden 1997), and a previous study found the model to be insensitive to even major changes in macroalgal growth rate (Mumby *et al*. 2006b). Secondly, the parameterization of fish grazing in shallow reefs did not explicitly include species in the family Acanthuridae. Acanthurids comprise around 9% of the grazer

biomass in mid-shelf reefs but up to 20% in shallow reefs (Mumby, unpublished data from Belize and the Bahamas). By ignoring the greater contribution of these fishes in shallow reefs, the model may have underestimated actual levels of grazing. However, an underestimation of grazing has little impact on the conclusions because even 49–57% grazing appeared to prevent unstable equilibria. Thirdly, hurricane impacts parameterized for mid-depth reefs were assumed to be identical to those in the shallower zone. In general, hurricane effects would be expected to be greater in shallower water because wave-power, which can dislodge and shatter corals, declines with increasing depth (Massel & Gourlay 2000). In the case of this model, however, it seems unlikely that such impacts would have been underestimated heavily for shallow water. This is because the parameterization for mid-depth reefs was generated from two of the most severe events in the 20th century, in which corals were scoured intensively by entrained sand (i.e. by using severe hurricanes, the parameterization will tend to over-estimate the impact of average hurricanes). Lastly, it should be borne in mind that the model did not include corals with a branching morphology and a later study will incorporate the effects of disturbance on *A. palmata* in shallow water and *A. cervicornis* on mid-depth reefs.

Mangroves in the Americas are currently being deforested at a faster rate than rainforest (Valiela, Bowen & York 2001), yet they appear to play a pivotal role in coastal and fisheries dynamics (Manson *et al*. 2005). Mangroves are often cited as protecting coral reefs from the efflux of sediment from estuaries (Ogden 1997). Here, we show that mangrove-based ontogenetic migrations of parrotfish may, through a trophic cascade on macroalgae, enhance the recovery rate of mid-shelf reefs from hurricanes. This conclusion is particularly significant given concerns about rising frequencies of intense hurricanes that may be linked to climate change (Knutson *et al*. 2001; Webster *et al*. 2005).

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Basic parameterization of simulation model for mid-shelf reefs with no mangrove connectivity

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2664.2008.01459.x
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